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Vertical Transmission in the Trematoda

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ABSTRACT: Vertical transmission is defined as contagious distribution of a symbiotic, sometimes infectious, agent from one generation of host to the next. With respect to helminths, vertical transmission is not common because contagion (i.e., direct transmission of an infectious agent between 2 members of the same host species) is rare; the overwhelming majority of helminth life cycles, even those that are called direct, require some form of additional development outside the host before the infective stage is reached and a return to the host is possible. Of 38 helminth species for which there is some evidence of vertical transmission, only 6 are trematodes. Two species, *Fasciola hepatica* and *Schistosoma japonicum,* have been reported to undergo vertical transmission through prenatal routes. Although the metacercariae and schistosomules of these respective species undergo somatic migration in mammals, there is neither evidence that their movement is directed to the fetus nor that they can become hypobiotic and capable of queuing for a future pregnancy, characteristics common to other species that rely on vertical transmission for a substantial part of their maintenance. Consequently, these infections are interpreted as aberrant migrations during pregnancy. Four species, *Alaria alata, A. marcianae, Pharyngostomoides adenocephala,* and *P. procyonis,* undergo vertical transmission postnatally via the milk and there is ample evidence available to suggest that this is a significant mechanism in their life cycles. The infective agent transmitted through the milk is the mesocercaria and this stage is capable of prolonged hypobiosis in the tissues of the female. Lactating females that are infected with mesocercariae serve primarily as paratenic hosts. This is true even in those host species that are usually regarded as definitive hosts. The term "amphiparatenesis" is used to describe the pattern of parasite transmission between 2 members of the same host species, 1 serving as a paratenic host (the mother) and the other as a definitive host (the offspring), and in which vertical transmission is the mechanism.

KEY WORDS: *Alaria* spp., endosymbiosis, milk-borne transmission, *Pharyngostomoides* spp., vertical transmission.

Infectious agents usually have limited mobility and must rely to a large part on the habits of their hosts for transmission. Some rely on "horizontal transmission" and infect contemporary hosts by employing vectors, seeding migratory pathways, or intertwining themselves in the food web of the target host. Others use "vertical transmission" and infect noncontemporary hosts. Vertical transmission connotes passage in time and is defined herein as contagious distribution of a symbiotic, sometimes infectious, agent from one generation of host to the next.

Vertical Transmission and Endosymbiosis

Although many believe that vertical transmission is rare and utilized by few organisms, it was noted in an earlier review on the subject that this is not so (Shoop, 1991). In fact, it could be argued that vertical transmission is the most common form of transmission in nature. The endosymbiotic theory suggests that mitochondria are the offspring of bacteria that were phagocytized by our ancestors eons ago. Some of these bacteria possessed mechanisms by which they survived in our ancestors and became symbionts. Some even possessed mechanisms by which they contributed to the survival of our ancestors. At some point, rather than relying on phagocytosis to enter the host, a mechanism developed whereby these bacteria were vertically transmitted from generation to generation in our ancestors. This intimate symbiosis and transmission has now proceeded to such a point that we hardly recognize the bacteria as distinct entities any longer. Covertly, vertical transmission of the bacteria/mitochondria lineage(s) occurs every time a eukaryote, whether plant, animal, or fungus, reproduces.

Vertical Transmission and Helminths in General

With respect to helminths, vertical transmission is rare because it entails true contagion, i.e., direct transmission of an infectious agent between 2 members of the same host species. The overwhelming majority of helminth life cycles require some form of additional development outside the host. For some, this additional development takes place in a prolonged free-living state, and for many, intermediate hosts, paratenic hosts, or vectors are required before returning to the same host species. Nonetheless, evidence for vertical transmission has been presented for 38 helminth species and has been re-

viewed by Baer (1972), Stone and Smith (1973), Hubbert et al. (1975), Stoye (1976), Miller (1981), Loke (1982), Macchioni and Tosi (1984), Shoop (1991), Conn (1994), and Lyons (1994).

Although not all of the evidence for the 38 species is convincing, 5 phylogenetic lines of helminths employ vertical transmission as a significant mechanism in their life cycles and include the hookworms, ascarids, protostrongylid lungworms, intestinal threadworms, and diplostomid flukes. Despite great differences in the life cycles of these helminths, the following 6 generalities with regard to vertical transmission can be made: (1) it is known to occur only in mammalian hosts; (2) transmission is strictly from the maternal side; (3) only larval parasites are involved; (4) there is an obligate somatic migration on the part of the parasite; (5) the transmitted stage shows substantial capacity for hypobiosis (temporary arrested development); and (6) the same stage infective to the mother is the stage that passes to the offspring.

Vertical Transmission and Trematodes

Of the 38 helminth species for which there is some evidence of vertical transmission, only 6 are trematodes (Shoop, 1991). Four of these species, *Alaria alata, A. marcianae, Pharyngostomoides adenocephala,* and *P. procyonis,* undergo postnatal transmission through milk and there is ample evidence available to suggest that this is a significant mechanism in their life cycles.

Two other species, *Schistosoma japonicum* and *Fasciola hepatica,* have been found in fetuses and neonates at times that, if based on the theoretical prepatent period of these worms, would have ruled out all but prenatal infection. Narabayashi (1914) was able to show experimental vertical transmission in several species of laboratory hosts with *S. japonicum* and the migrating schistosomule was the infective agent. However, prenatal infection among the schistosomes has not been found to be a significant pathway in nature even though it is not uncommon for schistosomules to migrate to maternal vessels associated with the placenta (Bittencourt et al., 1980). Prenatal infection of young calves with *F. hepatica* has also been documented, but the reported prevalences are usually quite low and variable. Stoye (1976) reviewed the subject and found most prevalences to be less than 2%. For example, Rees et al. (1975) examined the livers of 16,667 1–3-wk-old calves in Australia and found *F. hepatica* in 84 livers (prevalence of 0.5% and a total of 108 worms). Interestingly, a more recent report by Pecheur (1984) stated that 40% of 3–8-wk-old calves were positive for *F. hepatica* eggs from several farms in Belgium. The disparity between these prevalences is presently inexplicable. Metacercariae of *F. hepatica* are known to migrate to sites other than the liver (Boray, 1969), but there is neither evidence that their movement is directed to the fetus nor that they can become hypobiotic and capable of queuing for a future pregnancy. Consequently, these infections are categorized tentatively as aberrant migrations of the metacercariae during pregnancy; but it is important to recognize that we may be observing the primitive explorations of a parasite whose behavior could become genetically fixed should it provide fitness advantages.

At this time, however, trematode life cycles in which vertical transmission is both a clear strategy and significant part of the maintenance of the organism in nature are known only from species that undergo milk-borne transmission.

Phylogeny of *Alaria* and *Pharyngostomoides*

In a previous review of trematode transmission patterns, it was indicated that the only known cases of milk-borne transmission occur in the order Strigeiformes (Shoop, 1988). In a subsequent study, this was examined in greater detail (Shoop, 1989), and it was shown that *Alaria* and *Pharyngostomoides* are closely related genera in the family Diplostomidae. Among the characters that these genera share is the presence of a mesocercarial stage. This stage is known from only 4 genera: *Alaria, Pharyngostomoides, Procyotrema,* and *Strigea.* There is yet no evidence for milk-borne transmission in *Procyotrema* and no possibility of such in *Strigea,* a genus whose members infect birds.

Mesocercaria

The mesocercaria is the infective agent in the Trematoda that is vertically transmitted in the milk (Fig. 1). As the name indicates, it is a stage intercalated between the cercaria and metacercaria. Morphologically, it appears as an enlarged cercarial body that is characterized by a large number of small, posteriorly oriented surface spines and by 4 large, unicellular penetration glands. Temporally, the mesocercaria can live for years in a hypobiotic state in paratenic hosts and may be shuttled through various trophic levels.

The obligative somatic migration that occurs in mammals combined with the extraordinary capacity to undergo prolonged hypobiosis contribute to the singular ability of the mesocercaria to utilize milk-borne transmission as a strategy in the Trematoda.

Vertical Transmission in *Pharyngostomoides* Spp.

The life cycle of *Pharyngostomoides* spp. includes raccoons, *Procyon lotor,* as definitive hosts (Fig. 2). Within the definitive host there is a complex intestine–lung–intestine migration whereby the ingested mesocercaria migrates to the lungs and develops to the metacercarial stage. The metacercaria then migrates up the trachea, is swallowed, and matures to the adult worm in the small intestine. Eggs produced by adult worms are defecated into the environment, embryonate, and the resulting miracidia seek and penetrate aquatic snails of the genus *Menetus.* Several sporocyst generations ensue in the mollusc with the culmination of free-swimming cercariae. The cercariae penetrate or may be ingested by branchiobdellid annelids, which are symbiotic on crayfish, and develop to mesocercariae. When crayfish are ingested by raccoons, the symbiotic branchiobdellids are carried into the digestive tract of the vertebrate as well. The complex intestine–lung–intestine migration then completes the life cycle (Miller, 1981). Historically, it has been believed that paratenic hosts play no part in these life cycles.

A peculiar twist to the *Pharyngostomoides* spp. life cycle was presented in 1967 when it was suggested that vertical transmission from captive raccoons to their young had occurred (Harris et al., 1967). Three raccoons were both naturally infected with *Pharyngostomoides* spp. and pregnant when captured. In the laboratory, they were fed a diet devoid of any stages of *Pharyngostomoides* spp. and their young were nursed by them. The observations showed that a single pup born to and nursed from a female in 1961 had 78 adult *P. procyonis* in the intestine by the third month of life. In 1964, 3 pups were born to and nursed from a second female and again all were infected with adult worms by the third month of life; 1 pup was euthanized and 1,753 adult worms were found in the small intestine. And in 1966, a third female gave birth to a dead pup that was uninfected. In this latter case, the mother was infected and live mesocercariae were observed in her mammary gland secretions. The authors' conclusions from these 3 cases were that vertical transmission had occurred, and that it most likely involved a milk-borne route.

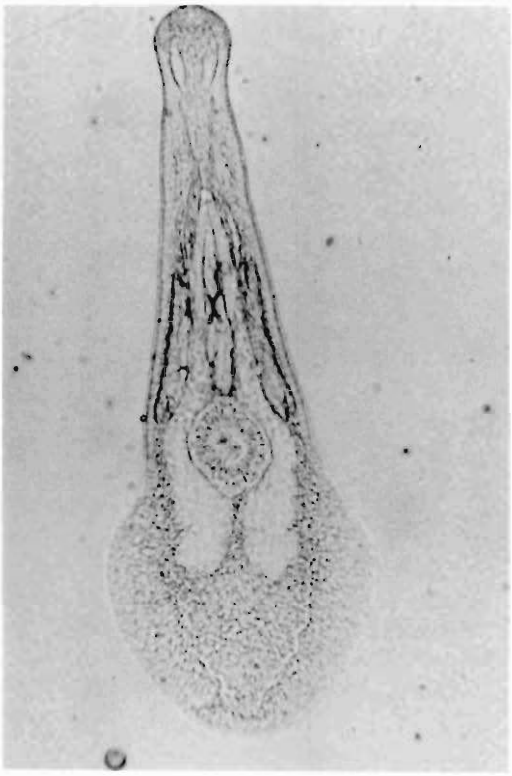

Figure 1. Living mesocercaria of *Alaria marcianae* after recovery from a reptilian paratenic host, *Agkistrodon piscivorus.*

In studying the life cycle of *Pharyngostomoides* spp., Beckerdite et al. (1971) reported that 2 species, *P. procyonis* and *P. adenocephala,* occurred in the genus and that both were probably vertically transmitted. However, they neither offered any further data for this belief nor mentioned the mesocercarial stage.

No further publication on vertical transmission of trematodes was released until 1981 when data were presented showing that multiple litters born to 2 captured, naturally infected raccoons became infected with *Pharyngostomoides* spp. (Miller, 1981). In 1 female, all neonates in the first 7 litters born to her which nursed became infected, while 3 of 5 neonates became infected in the eighth litter, and none was infected in the ninth litter. A similar pattern was observed for the second naturally infected female and her lit-

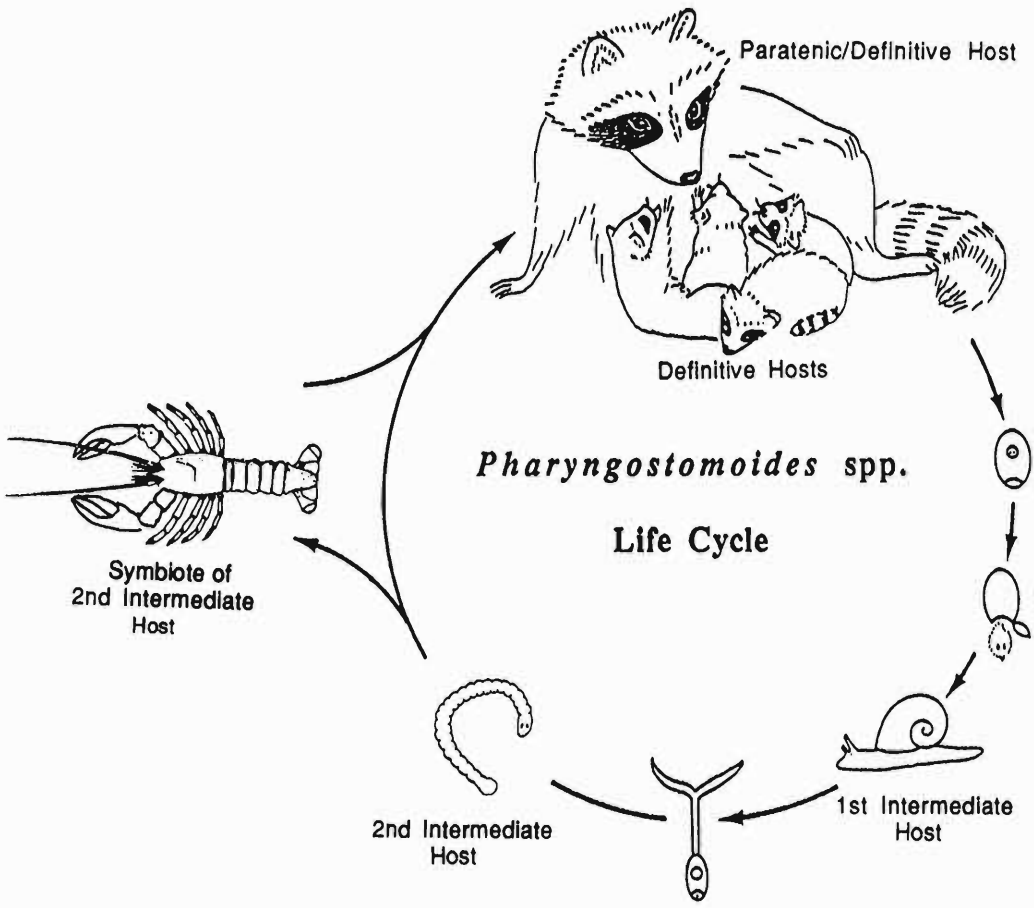

Figure 2. Life cycle of *Pharyngostomoides* spp.

ters. These data established unequivocally that (1) some form of vertical transmission had occurred, (2) the mechanism producing 100% infection of sequential litters was not trivial, (3) the mesocercariae had survived in the tissues of the females for many years, and (4) once a female was infected with mesocercariae, she was most probably infected for life. Although prenatal infection could not be ruled out as a possible source of these infections, the author clearly felt that they were the result of milk-borne transmission and cited the fact that several late-term fetuses and neonatal raccoons from other infected mothers were not infected, thus negating any form of prenatal transmission.

Although paratenic hosts have not been cited in previous work on *Pharyngostomoides* spp., these data suggest that they do play a major role in their life cycles, but not in the usual sense. It should be noted that the lactating raccoon is a paratenic host because mesocercariae ingested by her are transmitted without any further development in the milk. It is in the neonatal raccoons where development of these transmitted stages occurs.

Vertical Transmission in *Alaria* Spp.

Life cycles of the genus *Alaria,* although fundamentally similar to *Pharyngostomoides,* are more complicated because of the different species that can be definitive hosts and, more importantly, because of the number of paratenic hosts that may be involved in the life cycles (Pearson, 1956; Johnson, 1968) (Fig. 3). Usually, domestic or wild species of felines or canines are definitive hosts and, as in *Pharyngostomoides,* there is a complex intestine–lung–intestine migration (Shoop and Corkum, 1983a, 1984a). The

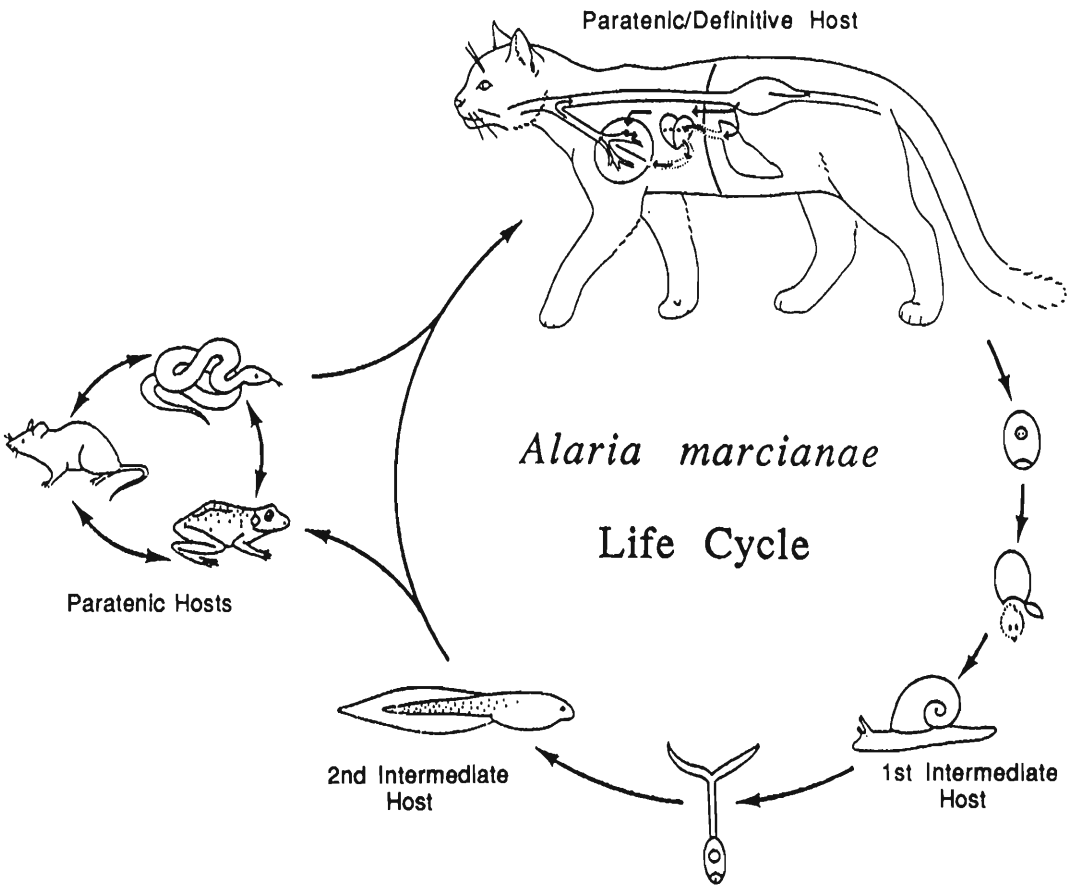

Figure 3. Life cycle of *Alaria marcianae*.

ingested mesocercaria migrates to the lung where development to the metacercaria takes place. The metacercaria then migrates up the trachea, is swallowed, and maturation to the adult worm occurs in the small intestine. Eggs produced by the adult worm are defecated into the environment, embryonate, and the resulting miracidia infect aquatic snails such as *Helisoma*. After several sporocyst generations in the mollusc, cercariae are released. The free-swimming cercariae penetrate the epidermis of tadpoles and develop to mesocercariae. At this point, 2 pathways exist. The tadpole could be ingested by the definitive host and the complex intestine–lung–intestine migration would lead to the adult worm. However, because few feline or canine hosts feed on tadpoles, it is more common for the mesocercariae to enter the paratenic pathway and be shuttled from 1 host to another without any development. The paratenic spectrum involves amphibians, reptiles, birds, and mammals, including man. Ultimately, the mesocercariae along with the paratenic host is ingested by the feline or canine definitive host and the intestine–lung–intestine migration then results in adult worms. Until the discovery of vertical transmission in *Alaria* spp., infection of man in modern times had usually been regarded as a dead-end for the mesocercaria.

My work on *Alaria* spp. began as a result of a human infection in Louisiana (Beaver et al., 1977) and culminated in an epidemiological study in 1981 (Shoop and Corkum, 1981). Numerous hosts were field-collected and examined for natural infections of *A. marcianae*. Experimental infections were also conducted in the laboratory to determine the range of possible hosts. One of those experimental infections included a female cat that was subsequently discovered to be pregnant. She was removed from study and returned

to a sixth floor vivarium to give birth. Several months after parturition, routine check of feces of all cats in the vivarium revealed eggs typical of *A. marcianae* in the feces of 2 kittens. At the time, the infection of these kittens was inexplicable, but records showed them to be the offspring of the female that had been given the experimental infection. Subsequent necropsy confirmed that both of these kittens were infected with adult *A. marcianae* in their small intestines. Necropsy of the female revealed mesocercariae in her mammary glands and adult worms in the small intestine. Although the source of infection for the neonates appeared to be from the milk, the possibility of prenatal infection could not be ignored.

At that point, it was decided to attempt an experiment in mice rather than to continue in cats (Shoop and Corkum, 1983b). The short gestation and suckling time as well as the ability to examine greater numbers of mice were primary reasons. The experiment was comprised of 3 major groups. Group 1 was designed to examine only the possibility of prenatal transmission. Five females were mated and infected with 150 mesocercariae each. Immediately at birth, the neonates were removed before suckling and both they and their dams were examined for mesocercariae. Group 2 was designed to examine the possibility of postnatal transmission. Five females were mated, allowed to give birth, and immediately after birth they were infected with 150 mesocercariae each and then returned to their litters to nurse. At weaning, both the dams and their offspring were examined for mesocercariae. Group 3 was composed of 5 virgin female mice each infected with 150 mesocercariae. These mice remained unmated and were examined for the presence of mesocercariae at the same time the females from the other groups were examined.

Results from Group 1 showed that none of 53 young born to the 5 prenatally infected females became infected. When the dams were examined it was found that all had become infected but there was no development beyond the mesocercarial stage. The majority of mesocercariae from the dams were found in the anterior trunk musculature and fat. No worms were found in the uterus or surrounding organs. Results from the females from Group 3 were essentially the same.

To the contrary, all 38 young nursed by dams infected postpartum in Group 2 became infected. When their dams were examined, it was found that the preponderance of worms occurred in the mammary glands. Histologically, worms were not only documented in the mammary glands of the dams, but also in their milk. As in the previous groups, however, there had been no development beyond the mesocercarial stage.

In summary, prenatal transmission had been negated as a factor in the mice; no infection of any offspring occurred in Group 1 and there was no association between the mesocercariae and the uterus or surrounding organs of the dams. Instead, it was found that 100% infection of offspring from 5 litters that suckled from infected dams had resulted. Moreover, there was a predilection of mesocercariae for the mammary glands of the lactating mice and the fact that these stages were also observed in the milk was incontrovertible evidence for milk-borne transmission in these paratenic hosts. Since those initial data, we have repeated these experiments in mice as well as rats and have found the same results each time (Shoop and Corkum, 1984b, c). Independent tests conducted in Russia on a closely related species, *A. alata,* in mice and rats have verified these findings (Sharpilo and Tkach, 1989).

Subsequently, similar experiments were conducted by us in cats, albeit with lesser numbers. To date, no prenatal transmission has been observed in these hosts either. Contrarily, every kitten nursed from infected female cats has become infected and mesocercariae have been recovered from the mammary glands of the females that nursed them. The only difference relative to the rodents is that the vertically transmitted mesocercariae develop to metacercariae in the lungs and then to adult worms in the small intestines of the kittens. What the stimulus is that draws the mesocercariae from the normal intestine–lung–intestine migration and to the mammary glands in the lactating cat, or the lactating female of any species, is not presently understood. However, the dependability of the transmission mechanism would have to be great for the parasite to forego reproductive maturity in what would otherwise appear to be a "good" definitive host only to risk dissemination to a new group of hosts.

This peculiar ability of a parasite to use an otherwise capable definitive host as a paratenic host and the young as definitive hosts is not unique to either *Alaria* or *Pharyngostomoides.* This pattern also occurs in species such as *Toxocara canis, T. cati, T. pteropodis, T. vitulorum, Strongyloides stercoralis, S. ransomi, S. ratti, S. westeri, Ancylostoma caninum,* and *Uncinaria*

lucasi. The process that produces these life cycle patterns is vertical transmission. We considered the pattern and process important enough to name. "Amphiparatenesis" was defined as the pattern of parasite transmission between 2 members of the same host species, 1 serving as a paratenic host (the mother) and the other as a definitive host (the offspring), and in which vertical transmission is the mechanism.

To understand more about amphiparatenesis in *A. marcianae,* we (Shoop and Corkum, 1987) conducted a study in cats similar to that reported for *Pharyngostomoides* spp. in raccoons (Miller, 1981). A female cat was infected experimentally postpartum with 800 mesocercariae of *A. marcianae* and allowed to return to her litter and nurse. After 21 days of nursing, all 5 of her kittens became infected and adult worms were found in their small intestines. There was no possibility of prenatal infection in this first litter. This female was then mated by males in our vivarium and produced 7 additional litters over 3 yr. All 5 kittens in the second litter, all 5 in the third litter, all 5 in the fourth litter, 1 of 4 in the fifth litter, and none of 5 in the eighth litter which nursed became infected. The female destroyed her sixth and seventh litter shortly after birth before they could be examined. However, kittens born dead in the second, third, and fourth litters were examined and none was infected. All infections in kittens that nursed resulted in either metacercariae in the lungs or adult worms in the small intestine. Over 25% of the initial inoculum given to the female cat was recovered from the first litter, and then lesser amounts were recovered through the course of litters until it appeared that the female was exhausted of worms. The amphiparatenic strategy of the worms resulted in the contagious infection of 21 offspring over the course of 3 yr. The female served primarily as a paratenic host and her offspring as definitive hosts.

Studies by Pence and Windberg (1984) have illustrated the significance of this amphiparatenic strategy in nature. They examined 177 coyotes, *Canis latrans,* in Texas and found 2 of the most common parasites to be *A. marcianae* and *A. caninum*; 128 coyotes were infected with the former and 175 by the latter. Furthermore, these species were the only 2 of a total of 20 observed that showed age-dependent overdispersion in young hosts. Rank abundances for *A. marcianae* and *A. caninum* were greater in pups than they were in juveniles, and greater in juveniles than they were in adult coyotes. The authors clearly believed this pattern resulted from vertical transmission and stated that "it is particularly significant that both of the helminth species demonstrating marked age dependent overdispersion . . . are capable of transmammary transmission."

Later, Pence et al. (1988) demonstrated that vertical transmission did occur in coyotes. A captured female coyote with natural infections of both *A. marcianae* and *A. caninum* was bred in captivity and gave birth to 5 pups. The pups nursed for 22 days and were then necropsied. All 5 became infected with both *A. marcianae* and *A. caninum.* Consequently, the population patterns of these 2 helminths, which had been observed previously in the 177 coyotes, could be clearly attributed to vertical transmission.

In the normal life cycles of species of *Alaria,* 3 orders of mammals can be infected by mesocercariae: rodents, carnivores, and primates. Rodents, as have been shown, usually serve as paratenic hosts and carnivores usually serve as definitive hosts, that is as long as they are not lactating. Primates, specifically man, have been infected on only a few occasions and although little information is known, it does appear they are paratenic hosts. Because of our epidemiological interests in *A. marcianae,* we investigated the nature of infection in primates to determine if vertical transmission could occur. We used callitrichid monkeys (Shoop et al., 1990). A single female was inoculated with 600 mesocercariae of *A. marcianae* 10 days after parturition and she was returned to her litter of 2. She showed signs of severe mesocercariasis in the first few days after infection and euthanasia was considered. She recovered, however, without intervention after several days, but neglected her infants, only feeding them occasionally. The offspring were necropsied 4 wk postinoculation of the mother and both were infected with a total of 16 mesocercariae. This same female was then mated again without further infection and produced triplets. One died the first day without nursing and was found uninfected at necropsy. The other 2 nursed normally for 5 wk before they were necropsied. Both had become infected and a total of 115 mesocercariae were recovered. Interestingly, 1 metacercaria was discovered in the lungs and 3 young adults were found in the small intestine of these young monkeys.

When the female monkey was necropsied 246 mesocercariae were recovered from numerous tissues. Histological examination of her mam-

mary glands revealed 36 mesocercariae. Many were in pools of milk and near lactiferous ducts in proximity to the nipple. Thus, the adult monkey served only as a paratenic host, as does man, and vertical transmission occurred to all offspring of 2 sequential litters that nursed. Prenatal transmission was not possible in the first litter and did not occur in the infant born dead in the second litter. What is curious about this infection is that although >99% of worms in the offspring remained mesocercariae, there was a small number that was apparently undergoing, or that had already undergone, a somatic migration leading to adulthood. How or why these few made it to adulthood is not presently understood. Nonetheless, the significance of these results was clear; that is, vertical transmission of these worms in humans is a distinct possibility. Therefore, an infected human is not necessarily a dead-end for this parasite!

Perhaps the most startling discovery in vertical transmission of trematodes occurred when it was found that vertical transmission of *A. marcianae* mesocercariae from lactating mice to their offspring did not stop at the F_1 generation (Shoop and Corkum, 1984b). It was observed that females of the F_1 generation, which had acquired infection through nursing from their mothers, were capable, in turn, of infecting their own offspring, the F_2, during lactation. This ability to transmit an infectious agent from generation to generation to generation in paratenic hosts represents the ultimate in paratenesis. It was also found that vertical transmission of the same agents in cats stopped at the F_1 generation because the worms developed to maturity in the kittens and were spontaneously passed some months thereafter.

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This review is dedicated to Dr. Grover C. Miller, University of North Carolina State University, on the year of his retirement. His contributions greatly enhanced our understanding of vertical transmission specifically and trematode life cycles in general.

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Directory of Parasitologists

Electronic communications provide a rapid means of obtaining information from or sending information to colleagues involved in parasitological research. However, there is currently no centralized "directory" that provides the e-mail addresses and FAX numbers of parasitologists. Dr. Peter Pappas is beginning to put together such a directory and invites all individuals involved in parasitological research to communicate with him in order to be included.

In addition to e-mail addresses and FAX numbers, this new directory will also include mailing addresses, telephone numbers, research interests, etc. As the directory grows and is updated, it will be sent electronically to everyone whose name appears in it (and who has provided an e-mail address), thus providing parasitologists with the most current available. For those individuals not currently using electronic mail, Dr. Pappas plans to make the directory available on disk at a later date.

Interested persons can contact Dr. Pappas via e-mail and he will forward additional information (a questionnaire) to them. Readers who do not have an e-mail address but wish to be included in the directory can contact Dr. Pappas by mail or FAX.

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